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Radial Maze Proficiency of Adult Wistar Rats Given Prenatal Complex Magnetic Field Treatments

ABSTRACT: *Exposure to sinusoidal (power-frequency) magnetic fields during prenatal development is implicated in adulthood behavioral impairments. However, the effects of prenatal exposure to weak-intensity, nonsinusoidal complex magnetic fields (CMFs), an increasingly common feature of the modern environment, have not been rigorously examined. In the present study, male and female Wistar-strain rats were exposed continually during prenatal development to one of three extremely low-frequency CMFs or a sham condition. As adults, rats were trained in an acquisition/reversal radial maze task. All rats exposed to the prenatal CMFs increased their commission of reference memory errors, but differences in working memory and motivation to complete the maze task were specific to the type of prenatal CMF. These results provide the first evidence that prenatal exposures to specific shapes of CMFs impair complex learning behaviors into adulthood.*
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The effects of extremely low-frequency (0.1–100 Hz), time-varying magnetic fields on fetal development have been investigated by manipulating either the amplitude or the frequency of the applied sinusoidal or square-wave fields. Several of these studies have revealed effects which may be related to the shape of the field, including disturbances in embryonic development (Delgado, Leal, Monteagudo, & Gracia, 1982; Ubeda, Trillo, Chacon, Blanco, & Leal, 1994), skeletal morphology (Huuskonen, Juutilainen, Julkunen, Maki-Paakkanen, & Komulainen, 1998; Huuskonen, Juutilainen, & Komulainen, 1993; Juutilainen, Huuskonen, & Komulainen, 1997), or behaviors (Persinger, 1969; Persinger & Pear, 1972). However, the temporal structure (shape) of the applied magnetic field rather than its intensity, per se, may be a critical factor for the induction of teratogenic effects (Juutilainen, Harri, Saali, & Lahtinen, 1986; Ubeda, Leal, Trillo, Jimenez, & Delgado, 1983). Some researchers may have failed to find significant results because they did not consider the shape of the applied wave form (Juutilainen et al., 1997; Maffeo et al., 1988; Maffeo, Miller, & Carstensen, 1984).

Many of the wave forms used in studies designed to discern the teratogenic effects of prenatal magnetic fields are symmetrically redundant and often applied at flux densities ranging from several microtesla (μT; 10 mG) to millitesla (mT; 10 G). A more recent approach is to employ magnetic stimuli with physiologically relevant wave forms applied at environmentally similar intensities to understand teratogenesis. These wave forms model neuronal firing and evoke biological effects through mechanisms which, because of the flux density of the applied fields, preclude current induction through known mechanisms. Convergent evidence from magnetic field modulations of memory processing (McKay, Persinger, & Koren, 2000) and evoked analgesia (Thomas, Kavaliers, Prato, & Ossenkopp, 1997a) suggest the effects of applied complex magnetic fields (CMFs) are specific to the temporal pattern or irregular shape of the wave form.

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We recently demonstrated the sensitivity of adult rats to exposure to acute magnetic field stimuli in radial maze tasks. We employed experimental configurations designed to simulate natural brain activity (McKay & Persinger, 2000) or the small (nT), minute-to-minute ambient variations in the intensity of the earth's magnetic field (McKay & Persinger, 1999). Because many prenatal manipulations influence radial maze performance, we reasoned that the radial maze might reveal effects in adulthood of magnetic field exposure during gestation. Here we show these effects. Moreover, we show that specific behavioral deficits in working memory, reference memory, and motivation are specific to particular prenatal CMF wave forms.

MATERIALS AND METHODS

Ninety-two Wistar rats (46 males, 46 females), approximately 4 to 6 months old, were used. Their parents (16 males, 32 females) were obtained from Charles River (Quebec). Rats were maintained 3 per cage in standard metal colony cages with food and water available ad libitum until 3 days before radial maze training, when rats were singly housed. Photophase onset was 0730 hr local time, with a 12:12 hr light:dark cycle. Ambient temperature was maintained at $20\pm1^{\circ}$C. All radial maze training was conducted during the early photophase.

Prenatal Magnetic Field Exposure

Male and female rats ($n=4$ and $n=8$, respectively, per treatment condition) were used as breeders and placed in a Plexiglas cage ($140\times33\times33$ cm) divided into four equal compartments. One male rat and 2 primiparous female rats were housed in each compartment. The 2 female rats were inserted at 5-day intervals; the male was removed 5 days after the second female was inserted. We assumed the 5-day interval was sufficient for the occurrence of one estrous cycle required for impregnation. At the ends of the cage were two identical and balanced 39×39 cm Helmholtz coils, each consisting of 305 m of 30 AWG (Belden 9978) wire wrapped in a single layer 18 cm wide (St-Pierre, Persinger, & Koren, 1998). The circuitry was designed such that only one coil could be activated during a given block of the experiment. The magnetic fields were presented 24 hr per day throughout the 21-day gestation period. Upon birthing, the mother and pups were relocated to a distant colony room.

Software operated on a Zenith XT computer converted a wave-form file of a few hundred to several thousand lines of digital values from 0 through 255 to analog equivalents of -5 V through $+5$ V, respectively. A graphical plot of the digital value (amplitude) against the line of the wave-form file (time) depicted the shape of the wave form. The voltage equivalent was propagated through the activated Helmholtz coil and emitted as a magnetic field. The duration that each line of the wave-form file was sent to the digital-to-analog converter (e.g., the pixel duration) as well as the time between each successive presentation of the wave form (e.g., the interstimulus interval) was controlled. The mean magnetic field intensities (standard deviations in parentheses) within each compartment over any 100-s interval with the field present were 510 nT (170 nT), 93 nT (25 nT), 32 nT (6.5 nT), and 21 nT (5 nT) from the compartment adjacent to the activated coil through to the compartment adjacent to the inactivated coil. These measurements were completed with a Metex 3800 multimeter and magnetic sensor probe (Electric Field Measurements, Stockbridge, MA) during a previous study (St-Pierre et al., 1998) and were verified during the present study. The intensity of the static geomagnetic field in the center of the treatment room, away from local distortions (e.g., shelving supports), was approximately 38,000 nT (FM 300 Vector Fluxgate Magnetometer).

Three complex magnetic wave forms and one sham condition were used. The first complex wave form, the frequency-modulated (FM) wave form (Thomas & Persinger, 1997), consisted of spikes of progressively decreasing frequency (15.9 to 10.1 to 7.1 to 5.6 Hz). Every second spike was presented at 56 Hz. The pixel duration and interstimulus interval for this wave form were 3 ms and 3 ms, respectively. This pulse has been shown to elevate nociceptive thresholds by acting through a delta-opioidergic pathway (Thomas, Kavaliers, Prato, & Ossenkopp, 1997b).

The second field, the multiple complex sequence (MCS) wave form (Persinger, St-Pierre, & Koren, 2001), was designed to intercalate temporally with calcium-mediated processes within cells. It consisted of numerous wave forms which are bioeffective. In fact, Smith, McLeod, Liboff, and Cooksey (1987) demonstrated increased transmembrane activity of calcium during exposures to specific weak magnetic fields when the fields temporally matched the ion resonance frequency for unhydrated calcium ions (Liboff, 1985). The pixel duration of our calcium-modeled wave form was set at 1 ms, the duration of each of the 50 complex patterns (employed in our previous research) that composed the complete wave form was 200 ms, the total presentation time of the entire wave form was 10 s, and the interval between presentations of each wave form was 40 s (see Persinger et al., 2001, for a detailed discussion of this wave form).

The third pattern, the theta-burst stimulation (TBS) pattern, was modeled after theta interval burst-firing which occurs in hippocampal pyramidal cells during spatial learning tasks (Otto, Eichenbaum, Wiener, & Wible, 1991). Microelectrode application of this wave form has been shown to enhance long-term potentiation (LTP) in vitro (Rose, Diamond, Pang, & Dunwiddie, 1988). The pattern consisted of a priming pulse followed 140 ms later by four pulses at 100 Hz. Sham exposures were conducted after the computer equipment had been disconnected from the Helmholtz coils. The four treatment conditions were completed one at a time over a 1-year period in the following order: FM, MCS, sham, and finally, TBS.

Radial Maze Training

The radial maze, designed after that by Olton and Samuelson (1976), consisted of a 60-cm-wide octagonal arena with eight 90×10 cm arms radiating outwards from each of the eight sides of the central arena; the arms and central arena were elevated 1 m above the floor. Extramaze visuospatial cues included tables, shelving, and equipment.

Forty-six male and 46 female progeny were randomly selected for radial maze testing from the litters that were exposed prenatally to FM ($n = 24$), MCS ($n = 28$), TBS ($n = 20$), and sham ($n = 20$) treatments. One or 2 rats of each gender were selected from each litter. Litter effects were not considered in the analyses due to the limited sampling of rats from each litter. They were singly housed and food deprived for 23 hr per day. Subjects were habituated to this schedule for 3 days before training began.

Rats were given one trial per day for 20 consecutive days in an eight-arm radial maze. During the 10-day acquisition period, odd-numbered arms were associated with reward (approximately 100 mg of crushed rat chow per arm). Following acquisition, subjects were trained for 10 days in a task-reversal period in which even-numbered arms were associated with reward. Rats were allowed a maximum of 15 min to eat or were removed immediately after consuming the rewards. The maze was thoroughly cleaned with aqueous acetic acid (0.4%) between trials.

Statistical Analyses

The total time to recover food rewards (to the nearest second), the number of reference memory error commissions (entering an arm not associated with reward), and the number of working memory error commissions (repeated entries into arms in the same trial) were the dependent variables. Data were analyzed with multivariate analyses of variance (MANOVA) with two levels repeated (10-day acquisition block vs. 10-day reversal block, day-by-day within blocks) and two levels not repeated (gender, prenatal treatments). Partial η^2 values were computed to estimate effect sizes. Post hoc analyses included one-way ANOVAs with Tukey's ($p < 0.05$) and correlated t tests, as appropriate. Polynomial trend analyses were performed to discern relationships between the intensity of each prenatally applied magnetic field wave form and the dependent measures. Because there were no systematic relationships between prenatal intensity and behavioral outcome as adults, intensity as an independent level in the analyses was omitted to conserve degrees of freedom. Analyses were performed with SPSS software operated through a VAX 4000 computer.

To insure that the sequence in which the treatments were completed did not confound the outcome of each treatment, we compared the sham group (males only) in the present study with a control group of 16 males selected from a procedurally identical study completed several months after the present study (McKay and Persinger, 2000). This latter study lasted only 8 days, and thus only the first 8 days of data from the present study were entered into the analyses. There were no statistically significant main effect differences between the sham group of the present study and the control group from our other study and no interactions between these two groups and trials for any of the dependent radial maze measures (data not shown).

RESULTS

The means and standard errors of the means (*SEM*s) for maze completion times and numbers of reference and working memory errors per daily trial are shown in Figures 1A, 1B, and 1C, respectively.

Maze Completion Times

The four prenatal treatment groups differed significantly in the length of time required to complete the maze, $F(3, 84) = 6.50$, $p = .001$, $\eta^2 = .19$. Post hoc analysis revealed this effect was due to longer maze-completion times for rats exposed prenatally to the MCS pulse relative to rats exposed to the FM pulse or sham conditions (which did not differ significantly) (Figure 2). Over the total 20 days of maze training, male rats required longer to complete the maze (mean = 5.82 min/day, $SEM = 0.31$ min/day) relative to female rats (mean = 3.67 min/day, $SEM = 0.17$ min/day), $F(1, 84) = 40.09$, $p < .001$, $\eta^2 = .32$, but interactions between prenatal treatment condition and gender were not evident, $F(3, 84) = 0.08$, n.s. All rats required less time per day to complete the maze during the second 10-day block of reversal training (mean = 2.68 min/day, $SEM = 0.15$ min/day) versus the first 10-day block of acquisition training (mean = 6.82 min, $SEM = 0.30$ min), $F(1, 84) = 512.50$, $p < .001$, $\eta^2 = .86$ (Figure 1A). Furthermore, the mean daily time required to complete the maze decreased significantly across days within each of the two 10-day training blocks, $F(9, 756) = 85.26$, $p < .001$, $\eta^2 = .50$ (Figure 1A). A three-way interaction between prenatal wave form, training block, and day of the training block was statistically significant, $F(27, 756) = 1.86$, $p < .01$. This interaction may be parsimoniously explained as an increase in time required to complete the maze during the first day of reversal training compared to the last day of acquisition training for sham, FM, and TBS prenatally treated rats. Rats exposed prenatally to the MCS wave form required equivalent times to complete the maze when the task demands changed (Figure 1A). This latter result indicates that a change in task parameters did not affect the performance of rats exposed prenatally to the MCS wave form, possibly suggesting the use of a nonspatial maze strategy for this group.

Reference Memory Errors

A difference in reference memory errors was found between the four prenatal magnetic field conditions, $F(3, 84) = 2.67$, $p = .05$. However, the source of this main effect appeared to be the interaction between prenatal magnetic field treatment and acquisition versus reversal blocks, $F(3, 84) = 9.06$, $p < .001$, $\eta^2 = .24$. Post hoc analyses (Tukey's, $p < .05$) showed the source of the interaction to be (a) the increased commission of reference errors during the 10-day acquisition block for rats exposed to the FM, MCS, and TBS wave forms

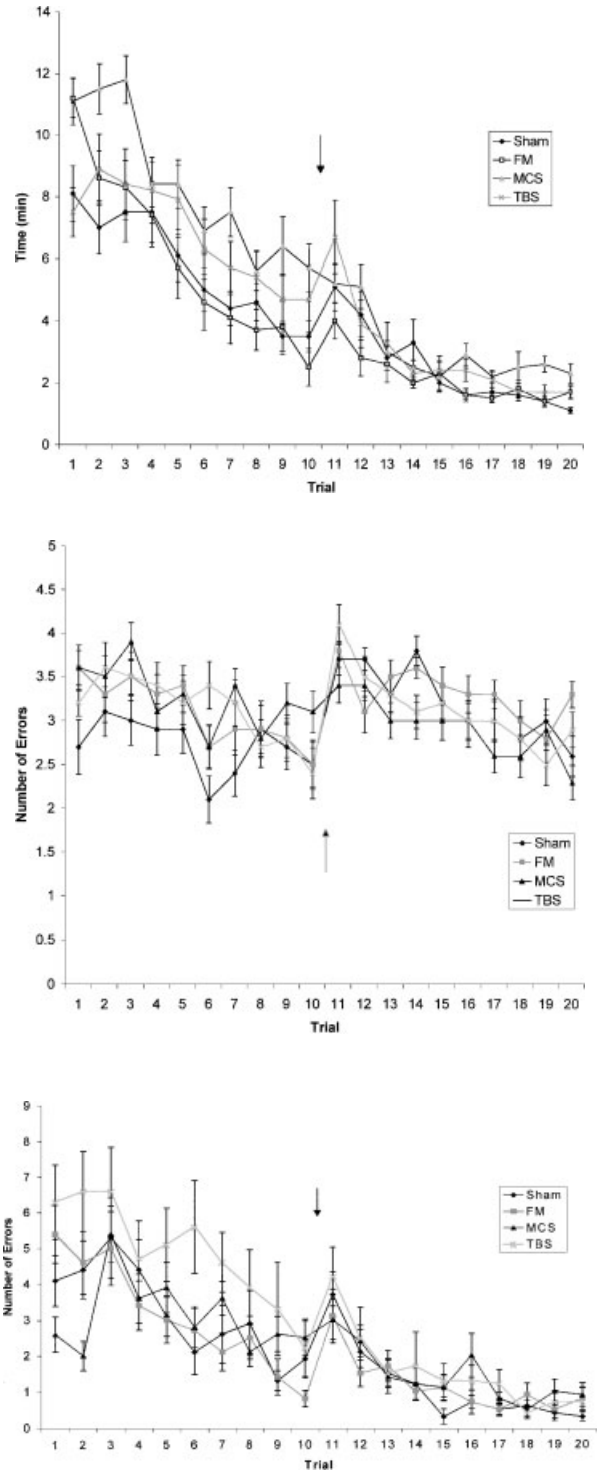

FIGURE 1 Mean (± SEM) maze completion times (in min) (**A**), number of reference errors (**B**), and number of working memory errors (**C**) during daily maze trials. Rats had been exposed prenatally to sham conditions or one of three complex magnetic fields [frequency-modulated (FM) wave form, multiple complex sequence (MCS) wave form, or theta-burst stimulation (TBS) wave form]. Arrows indicate transition from acquisition to reversal task.

(which did not differ from one another) relative to sham-exposed rats, and (b) fewer reference errors during the 10-day reversal block for rats exposed prenatally to the MCS wave form relative to FM and sham-exposed rats. FM and sham-exposed rats did not differ from one another (Figure 3). Fewer reference errors were committed across maze trials (days) within each 10-day block of training, indicating a learning curve, $F(9, 756) = 12.17$, $p < .001$ (Figure 1B). Male and female rats did not differ in reference errors, $F(1, 84) = 0.15$, n.s.; prenatal wave form did not interact significantly between genders, $F(3, 84) = 2.17$, n.s.

Working Memory Errors

Rats in the four prenatal magnetic field treatments differed in working memory, $F(3, 84) = 5.52$, $p < .01$, $\eta^2 = .17$. However, the source of this main effect was the interaction between prenatal magnetic wave form and training block (acquisition vs. reversal), $F(3, 84) = 8.15$, $p < .001$, $\eta^2 = .23$. Post hoc analysis showed more working memory errors were committed during the 10-day acquisition block by rats exposed prenatally to the TBS magnetic field compared to the other groups. The treatment groups did not differ in working memory errors during the 10-day reversal block (Figure 4). Working memory errors decreased within each block, $F(9, 756) = 22.68$, $p < .001$, $\eta^2 = .21$ (Figure 1C). Although gender did not differ as a main effect, $F(1, 84) = .05$, n.s., gender interacted significantly between the two 10-day training blocks, $F(1, 84) = 11.35$, $p = .001$. Mean daily working errors during the acquisition block for male and female rats were 3.79 errors/day ($SEM = 0.21$) and 3.31 errors/day ($SEM = 0.25$), respectively; during the reversal block, male and female rats committed 1.13 errors/day ($SEM = 0.10$) and 1.51 errors/day ($SEM = 0.17$), respectively. Although rats of both genders committed significantly fewer errors in the reversal block (mean = 1.32 errors/day, $SEM = 0.10$ errors/day) relative to the acquisition block (mean = 3.55 errors/day, $SEM = 0.16$ errors/day), $F(1, 84) = 297.92$, $p < .001$, $\eta^2 = .78$ (Figure 1C), the source of the interaction was the greater decrease in mean daily working errors for male rats between the two 10-day blocks (net change = 2.66 errors per block, $SEM = 0.21$) compared to female rats (net change = 1.80 errors per block, $SEM = 0.20$).

DISCUSSION

Magnetic fields evoke behavioral and biological effects that are specific to the temporal configurations of the applied fields. McKay et al. (2000) reported that

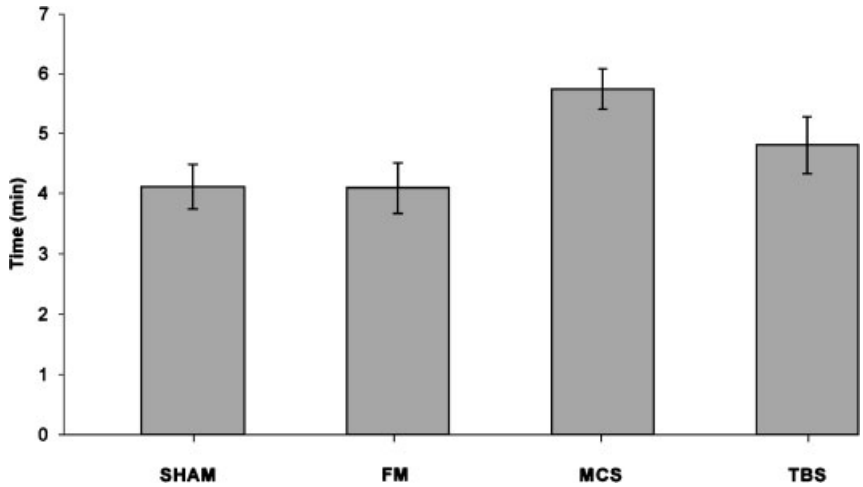

FIGURE 2 Mean (± SEM) maze completion times (in min) per trial averaged across all 20 trials for rats exposed prenatally to sham conditions, the frequency-modulated (FM) wave form, the multiple complex sequence (MCS) wave form, or the theta-burst stimulation (TBS) wave form.

postconditioning exposures to TBS-patterned CMFs, but not burst-firing or intensity-matched, extremely low-frequency sinusoidal magnetic fields, markedly attenuated the amount of learned fear to contextual stimuli for rats. Conversely, McPhee and Persinger (1998) found that acute exposures to burst-firing magnetic fields, but not TBS-patterned magnetic fields following daily radial maze sessions, decreased the time required for rats to complete the maze task without affecting reference and working memory errors. Wave-form–specific findings for behaviors in a radial maze task were revealed in the present study. Rats that had been exposed prenatally to the MCS wave form required longer times to complete the maze task while rats that had been exposed prenatally to the TBS wave form committed more working memory errors.

Contextual and spatial learning are known to involve different neuroanatomical regions (Good & Honey, 1997) and different pharmacological systems (McKay et al., 2002). This fact suggests that magnetic fields with specific patterns employed in our previous studies affected discrete neural structures or transmitter systems without gross whole-brain or multiple transmitter system generalizations. Likewise, pharmacological agents (ligands) evoke specific biological and ultimately specific behavioral effects because (a) the structures (receptors) to which they bind show high chemical specificity complementary only to appropriately structured ligands, and

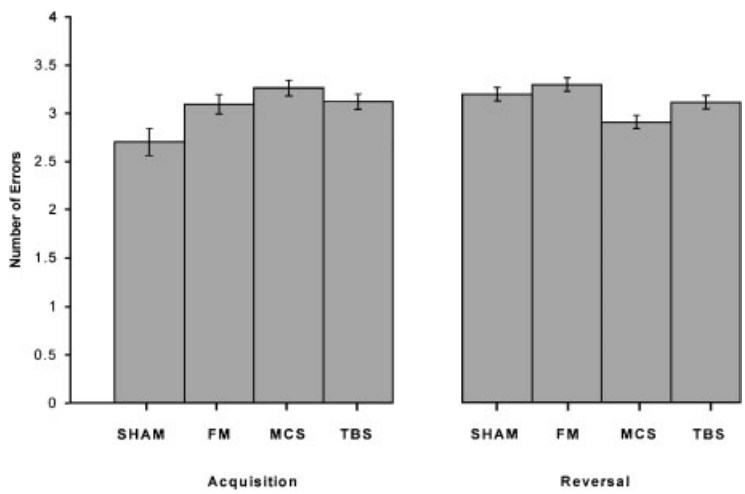

FIGURE 3 Mean (± SEM) number of reference errors per trial during acquisition and reversal blocks for rats exposed prenatally to sham conditions, the frequency-modulated (FM) wave form, the multiple complex sequence (MCS) wave form, or the theta-burst stimulation (TBS) wave form.

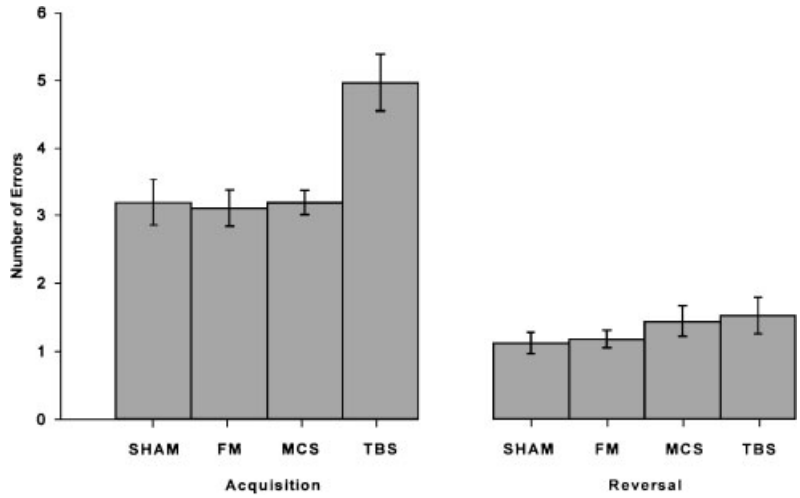

FIGURE 4 Mean (± SEM) number of working memory errors per trial during acquisition and reversal blocks for rats exposed prenatally to sham conditions, the frequency-modulated (FM) wave-form, the multiple complex sequence (MCS) wave form, or the theta-burst stimulation (TBS) wave form.

(b) there is hetereogeneous distribution of specific receptors and receptor subtypes throughout the nervous system. Magnetic fields with specific wave forms or temporal configurations may evoke specific effects because the neural systems they act upon require the type of specificity required for classic ligand-receptor interactions.

Classes of receptors (e.g., μ-, δ-, and κ-opioid receptors) respond to general agonists and antagonists, but receptor subtypes individually respond to subtype-specific ligands. Thus, depending upon the exact structure of the pharmacological or magnetic ligand, biological and behavioral effects may be unique to a particular subtype or generalized to a broader class of ligands. For instance, Thomas et al. (1997a, 1997b) demonstrated that a pulsed magnetic field, but not other CMFs, evoked analgesia by specifically augmenting delta-opioid function. Antagonists at mu- and kappa-opioid sites did not affect the magnetic field-evoked analgesia. Fleming, Persinger, and Koren (1994) and Ryczko and Persinger (2002) showed that the primarily mu-opioid antagonist naloxone partially attenuated the magnitude of CMF-evoked analgesia, although the magnitude of the attenuation for equivalent doses of naloxone differed between magnetic fields with different wave forms. We suggest that the effects of the MCS and TBS wave forms, given their unique effects on radial maze behaviors, were conceptually equivalent to a subtype-specific ligand. The observation that all complex wave forms increased commissions of reference errors may be equivalent to an effect on a broader class of receptors.

Slamberova et al. (2001) reported that chronic prenatal administration of the nonspecific opioid agonist morphine markedly increased the time required for both male and female rats to complete a radial maze task when tested as adults. This finding was comparable to the longer times to complete the maze observed in the present study for rats exposed prenatally to the MCS wave form. Slamberova, Szilagyi, and Vathy (2001) also noted that maternal behaviors decreased as a result of morphine administration during the prenatal period. Because adult female Wistar rats habituate behaviorally to applications of CMFs after approximately 2 days of 30-min/day sessions (Martin and Persinger, 2001), we consider the behavioral effects in the present study, which involved 24-hr/day exposures over 3-week periods, to be effects on prenatal development and not likely alterations in maternal behaviors.

The present study demonstrated that exposure of rats to CMFs applied during the prenatal period affected memory and learning when these animals were tested as adults. Several investigators have approached the study of magnetic field teratology by employing 60- and 50-Hz magnetic fields. These frequencies are epidemiologically relevant because they are the frequencies of power transmission in North America and Europe, respectively. Cumulative evidence indicates that the wave form, or the complexity, of the magnetic fields may in some cases be more important than specific frequencies or exposure intensities (Juutilainen et al., 1986; Persinger et al., 2001; Ubeda et al., 1983). Given the pervasiveness of anthropogenic 50- and 60-Hz magnetic fields, anomalies in transmission of these frequencies which effectively create higher and lower frequency ''pulses,'' and the interactions of these fields due to the spatial geometries of their household or industrial origins, the emergence of ''complex'' magnetic fields that have biological relevance

for both adult organisms—and from the present study, developing organisms—is highly probable. Ongoing research has been directed towards understanding the effects of prenatal CMF exposures at the cellular level and identifying pharmacological agents that when coadministered during magnetic field exposures antagonize the effects of the fields.

NOTES

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